

Loss of Glyphosate Efficacy: A Changing Weed Spectrum in Georgia Cotton

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Introduction of glyphosate resistance into crops through genetic modification has revolutionized crop protection. Glyphosate is a broad-spectrum herbicide with favorable environmental characteristics and effective broad-spectrum weed control that has greatly improved crop protection efficiency. However, in less than a decade, the utility of this technology is threatened by the occurrence of glyphosate-tolerant and glyphosate-resistant weed species. Factors that have contributed to this shift in weed species composition in Georgia cotton production are reviewed, along with the implications of continued overreliance on this technology. Potential scenarios for managing glyphosate-resistant populations, as well as implications on the role of various sectors for dealing with this purported *tragedy of the commons*, are presented. Benghal dayflower, a glyphosate-tolerant species, continues to spread through Georgia and surrounding states, whereas glyphosate susceptibility in Palmer amaranth is endangered in Georgia and other cotton-producing states in the southern United States. Improved understanding of how glyphosate susceptibility in our weed species spectrum was compromised (either through occurrence of herbicide-tolerant or -resistant weed species) may allow us to avoid repeating these mistakes with the next herbicide-resistant technology.

Nomenclature: Glyphosate; Benghal dayflower, *Commelina benghalensis* L.; Palmer amaranth, *Amaranthus palmeri* S. Wats; cotton, *Gossypium hirsutum* L.

Key words: *Amaranthus palmeri*, Benghal dayflower, *Commelina benghalensis*, glyphosate, herbicide resistance, herbicide tolerance, Palmer amaranth, tragedy of the commons, tropical spiderwort.

Herbicides are an important component in commercial agronomic cropping systems, but despite their use, weeds persist in agroecosystems. Weeds can escape herbicide control for many reasons, including: less-than-ideal environmental conditions (i.e., too cold, too windy, or too dry), problems associated with misapplication (i.e., improper calibration and herbicide rate, clogged nozzles, or weeds that are too large for control), and the occurrence of herbicide-tolerant and herbicide-resistant weeds. The evolution and spread of herbicide-tolerant and herbicide-resistant weeds will likely guide the direction of crop production in the future (Culpepper 2006). Of the 331 herbicide-resistant weed biotypes in the world, 125 occur in the United States, more than twice as many as Australia, the country with the second-most number of cases (Heap 2009). The widespread adoption of glyphosate-tolerant (GT) crops, and subsequent glyphosate use, on a significant portion of the available agronomic cropland has provided a strong selection pressure for weeds that are not controlled by glyphosate. The objectives of this review are to describe how the utility of glyphosate has been compromised, present some of the factors that have driven growers to overutilize glyphosate and GT crop technology (specifically cotton), and propose potential actions that may help avoid repeating these mistakes in the future.

Changes in Cotton Production in the Southeast United States.

Cotton production in the United States was drastically altered with the introduction of GT cultivars in 1997. Initial projections from 1998 were that GT cotton (GTC) cultivars would be grown on 40 and 50% of the hectares by 2000 and 2006, respectively (Shaner 2000). However, by 2000 glyphosate was the most commonly applied herbicide in cotton (applied to 56% of the U.S. cotton hectares), with greater than 75% of Georgia, Mississippi, North Carolina, and Tennessee cotton receiving at least a single POST

application every year (USDA-NASS 2001). In just 11 yr, producers in Arkansas, Georgia, Louisiana, Mississippi, Missouri, North Carolina, South Carolina, and Tennessee grew GTC cultivars and used glyphosate for POST weed control on greater than 95% of the hectares (USDA-NASS 2008). The rapid adoption of GTC cultivars mirrors that of hybrid corn cultivars in the United States in the 1930s (Miller 2008), demonstrating that growers will rapidly adopt technology that is perceived as beneficial.

Before the introduction of GTCs, growers typically used disk harrows and moldboard plows to eliminate weeds and prepare a field for crop planting. After planting, weed control was achieved through soil-applied and postdirected herbicides, and several cultivations. Cotton production using these methods required multiple trips across a field (i.e., additional costs associated with labor, fuel, and equipment usage) relative to GTC cultivars (Shurley 2006). In addition, crop production systems before GTC relied on the use of herbicides with registrations that have since been discontinued (e.g., cyanazine, methazole) or are under threat of discontinuation (e.g., MSMA).

Although there was a cost premium associated with GTC, the use of this technology provided many benefits to the growers who adopted it. Some of the positive characteristics associated with glyphosate are: (1) broad spectrum of weed control, (2) good herbicide movement into and translocation through susceptible plants (i.e., minimal weed regrowth), (3) flexibility of timing for weed control applications (i.e., 10-cm weeds are not too large for adequate control in most instances), and (4) a favorable environmental profile due to glyphosate's low volatility, short half-life, minimal movement to groundwater, and classification among the least toxic pesticides to animals (Duke and Powles 2008). The adoption of GTC technology has been associated with an increase in the number of cotton hectares planted, fewer applications of other herbicides, reduced tillage, and the almost exclusive use of glyphosate for weed control (Duke and Powles 2008; Powles 2008a). Reduced tillage promotes soil conservation and is beneficial to cropping systems because of increased water infiltration, improved soil moisture, reduced soil erosion and

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Table 1. Relative rankings of the most troublesome weeds in Georgia cotton in 1995 and 2005 (Dowler 1995; Webster 2005).

Ranking	1995	2005
1	Nutsedges	Benghal dayflower
2	Sicklepod	Palmer amaranth
3	Coffee senna	Morningglories (<i>Ipomoea</i> spp.)
4	Texas millet	FL pusley
5	Pigweeds	Nutsedges
6	Cocklebur	Asiatic dayflower
7	Morningglories (<i>Ipomoea</i> spp.)	Smallflower morningglory
8	Wild poinsettia	Texas millet
9	Bristly starbur	Wild poinsettia
10	Bermudagrass	Bermudagrass

herbicide loss, and reduced sandblasting of young seedlings due to wind erosion (Potter et al. 2004; Wilcut et al. 1993). Strip-tillage cotton can reduce approximately 30% of preharvest labor and machinery-related costs (Shurley 2006). GTC allowed Georgia farmers to lead the region in the adoption of conservation tillage practices, with 41% of cotton in conservation tillage in 2004, up from 12% in 1996 (CTIC 2005). For this same period, conservation tillage only increased from 12 to 22% for the other states combined across the rest of the Cotton Belt.

Shifts in Weed Species Composition. The composition and structure of weed communities in agricultural fields are altered in response to imposed selection pressures. The Southern Weed Science Society conducts an annual survey of university professors (extension specialists) to identify the most troublesome weeds (i.e., those that are most difficult to control or cause the greatest monetary losses) in various crops and natural areas. Changes in weed species composition between 1995 and 2005 (before and after the introduction of GTC, respectively) demonstrate how rapidly shifts in species composition can occur (Table 1). The surveys of the most troublesome weeds in Georgia cotton in 1995 and 2005 have five species (or complexes) in common: nutsedges (*Cyperus* species), morningglories (*Ipomoea* species), Texas millet [*Urochloa texana* (Buckl.) R. Webster], wild poinsettia (*Euphorbia heterophylla* L.), and common bermudagrass [*Cynodon dactylon* (L.) Pers.] (Dowler 1995; Webster 2005). Many of the changes in weed species composition over this period can be attributed to differences in management practices. For instance, sicklepod [*Senna obtusifolia* (L.) H.S. Irwin & Barneby], coffee senna [*Senna occidentalis* (L.) Link], common cocklebur (*Xanthium strumarium* L.), and Florida beggarweed [*Desmodium tortuosum* (Sw.) DC.], significant weed species as reported in the 1995 survey, are all susceptible to glyphosate and were absent from the 2005 ranks. These species were replaced by species not effectively controlled by glyphosate, including Florida pusley (*Richardia scabra* L.), Asiatic dayflower (*Commelina communis* L.), Benghal dayflower, and Palmer amaranth. The last two weeds on this list, ranked as the most troublesome weeds in Georgia cotton, consistently escape control with glyphosate and became problematic. Bengal dayflower is tolerant of glyphosate (Culpepper et al. 2004), whereas Palmer amaranth is resistant to glyphosate (Culpepper et al. 2006).

The Weed Science Society of America defines herbicide tolerance as “the inherent ability of a species to survive and reproduce after herbicide treatment. This implies that there was no selection or genetic manipulation to make the plant tolerant” (Anonymous 1998). Benghal dayflower is tolerant to glypho-

sate and many of the herbicides used in agronomic crops. It was first reported in agronomic fields of south Georgia in 1999, soon after the adoption of GTC (Culpepper et al. 2004). Benghal dayflower is currently found in 42 counties in Georgia, with reported occurrences in Florida, South Carolina, North Carolina, Alabama, Mississippi, and Louisiana (Culpepper et al. 2008a; Faden 1993; Krings et al. 2002; Webster et al. 2005). The distribution of Benghal dayflower outside of the United States includes Australia, Africa, Asia, the Pacific Islands, South America, and the West Indies (Webster et al. 2005). Studies have demonstrated that the mechanism of glyphosate tolerance of Benghal dayflower is reduced absorption and translocation (Monquero et al. 2004a; Monquero et al. 2004b), whereas another study determined that growth of Benghal dayflower was stimulated by glyphosate (Velini et al. 2008).

Benghal dayflower has a prostrate growth habit and the ability to reduce cotton and peanut yields up to 60 and 100%, respectively, through season-long interference (Webster et al. 2007, 2009). It is listed among the most troublesome weeds of cotton and peanut (*Arachis hypogaea* L.) in Georgia and Florida (Webster 2005). Although glyphosate is not currently used in-crop with peanut, cotton is a common rotation crop. Benghal dayflower is tolerant of numerous herbicides commonly used in peanut and cotton (Prostko et al. 2005), but sensitivity to metolachlor has allowed for effective control (Webster et al. 2006). The mode of action of metolachlor is related to cell division and growth of germinating seeds (Devine et al. 1993). Peanut is tolerant of metolachlor, whereas metolachlor has activity when applied PRE against both cotton and Benghal dayflower. However, Benghal dayflower is a tropical species, with the bulk of emergence occurring later in the season than most common agronomic weeds in Georgia (Webster et al. 2006). This delayed emergence pattern in Benghal dayflower allows metolachlor application after cotton emergence, but before Benghal dayflower germination. Growers also use the later emergence patterns of Benghal dayflower to avoid crop competition. Cotton is slow to establish and not very tolerant of weed competition soon after planting (Buchanan and McLaughlin 1975). When cotton was planted in mid-May, potential yield loss from Benghal dayflower was half of that of June-planted cotton (Webster et al. 2009). This combination of early cotton planting and use of metolachlor has allowed growers to continue cotton production in fields that have been invaded by Benghal dayflower.

The Weed Science Society of America defines herbicide resistance as the “inherited ability of a plant to survive and reproduce following exposure to a dose of herbicide normally lethal to the wild type. In a plant, resistance may be naturally occurring or induced by such techniques as genetic engineering or selection of variants produced by tissue culture or mutagenesis” (Anonymous 1998). Herbicides do not cause the mutations that lead to herbicide resistance, but instead impose selection pressure such that adaptive, naturally occurring mutations become established and increase in frequency in a plant population. Palmer amaranth has developed resistance to many classes of herbicides including glyphosate, dinitroanilines, triazines, and acetolactate synthase (ALS) inhibitors (Culpepper et al. 2006; Gossett et al. 1992; Heap 2008; Horak and Peterson 1995; Sprague et al. 1997; Vencill et al. 2008; Wise et al. 2009). In Georgia cotton, Palmer amaranth resistance to glyphosate and ALS-inhibiting herbicides is a

significant weed management issue. Native to the southwest United States, it is unclear when Palmer amaranth arrived in the southeastern United States. Palmer amaranth is an aggressive weed in cotton, with densities of 10 plants per 9.1 m of row reducing cotton yields at least 54% (Rowland et al. 1999). In addition to simply reducing cotton yield, Palmer amaranth will also hinder cotton harvest because of the inability of the mechanical harvesting equipment to navigate through Palmer amaranth stems that can grow to 10 cm in diameter. Although Benghal dayflower continues to spread throughout Georgia and is problematic where it occurs, Palmer amaranth is likely a greater threat for the southern cotton-producing region because of its aggressive growth habit and ability to evolve herbicide resistance. On the basis of their native habitats and current distributions throughout the world, we suspect that Palmer amaranth has a greater potential distribution in the United States than Benghal dayflower.

Palmer amaranth has been an economically important weed in Kansas, Oklahoma, and Texas since the early 1970s (Buchanan 1974). With the exception of North Carolina and South Carolina, Palmer amaranth was not singled out from other pigweed species as being troublesome in the southeastern United States before the use of GTC (Dowler 1995). In 2004 glyphosate-resistant (GR) Palmer amaranth was detected on a single farm in Macon County, Georgia and was the first documented case of glyphosate resistance in the species (Culpepper et al. 2006). By 2005 GR Palmer amaranth was found in two adjacent counties in central Georgia, 11 counties in North Carolina, and three contiguous counties of eastern Arkansas and western Tennessee (Culpepper et al. 2008b; Nichols et al. 2008). In 2006, GR Palmer amaranth was identified in six, six, and one additional counties in Georgia, Arkansas, and Tennessee, respectively (Culpepper et al. 2008b; Nichols et al. 2008). South Carolina GR Palmer amaranth was documented for the first time in 2006 (Nichols et al. 2008). By 2007 the occurrence GR Palmer amaranth increased by nine new counties in Georgia and seven new counties in Arkansas (Nichols et al. 2008). A 2005 survey of 290 North Carolina fields confirmed GR Palmer amaranth in 49 of them (Culpepper et al. 2008b). After the 2008 growing season, GR Palmer amaranth was found in 26 counties in Georgia, 11 counties each in North Carolina and South Carolina, and 1 county in Alabama; totaling an estimated 250,000 ha of agronomic land with GR Palmer amaranth in the southeastern United States (Culpepper et al. 2009). We estimate that most Georgia cotton-producing counties will have GR Palmer amaranth by the end of the 2010 growing season.

Palmer amaranth causes significant yield loss in agronomic crops (Klingaman and Oliver 1994; Massinga et al. 2001; Moore et al. 2004; Morgan et al. 2001), with a relatively low population density of two GR Palmer amaranth plants per 5.6 m² reducing cotton yields 23% (MacRae et al. 2008). In cotton, the current recommendations for managing GR Palmer amaranth in Georgia includes PRE mixtures of fomesafen, pyriithiobac, and pendimethalin followed by glyphosate and metolachlor POST, followed by a lay-by directed application of MSMA and diuron, for a total of seven different herbicide modes of action (Culpepper and Kichler 2009). A survey of Georgia growers revealed that the presence of GR Palmer amaranth in fields increased management costs

by 58%, from \$81 ha⁻¹ to \$129 ha⁻¹ (Culpepper et al. 2009).

Evidence suggests that the GR Palmer amaranth biotypes in the southeastern United States have variable resistance mechanisms. Susceptible plants treated with glyphosate accumulate high levels of shikimate, due to inhibition of 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS) in the aromatic amino acid synthesis pathway (Devine et al. 1993). The initial GR Palmer amaranth biotype from Georgia did not accumulate shikimate in the presence of glyphosate (Culpepper et al. 2006). The suspected mechanism of resistance in the Georgia GR Palmer amaranth biotype involves amplification of the EPSPS gene, a novel mechanism of resistance in weed populations (Gaines et al. 2009). In contrast, the Tennessee GR Palmer amaranth biotype accumulated shikimate in the presence of glyphosate, indicating that glyphosate inhibited EPSPS; the exact mechanism of resistance has not been determined.

In greenhouse studies, the Georgia GR Palmer amaranth biotype had a rate of glyphosate necessary to reduce growth 50% (glyphosate I_{50}) of 1.2 kg ae ha⁻¹, which was eight times greater than that of the susceptible biotype (I_{50} = 0.15 kg ha⁻¹) (Culpepper et al. 2006). However, field studies indicated that glyphosate applied at 12 times the recommended rate failed to control the GR biotype (Culpepper et al. 2006). Other research indicated that at least two GR Palmer amaranth biotypes in North Carolina had a glyphosate I_{50} between 0.18 and 0.36 kg ha⁻¹, two and four times greater than the susceptible biotype (I_{50} = 0.089 kg ha⁻¹). The most resistant biotype in North Carolina had a glyphosate I_{50} of 1.96 kg ha⁻¹, or 22 times the susceptible (York 2007). In Arkansas a GR Palmer amaranth biotype had a glyphosate I_{50} of 2.8 kg ha⁻¹ compared with 0.035 kg ha⁻¹ for the susceptible (Norsworthy et al. 2008).

GT Cropping Systems. A common characteristic of GT and GR weeds is that they developed in systems with little or no diversity in weed control practices (Powles 2008a). Weed species with a known tolerance to glyphosate include dayflowers (*Commelina* spp.), smartweeds (*Polygonum* spp.), and morningglories. Genetically diverse weed species, such as crabgrasses (*Digitaria* spp.), foxtails (*Setaria* spp.), *Sorghum* species, velvetleaf (*Abutilon theophrasti* Medik.), pigweeds (*Amaranthus* spp.), common lambsquarters (*Chenopodium album* L.), kochia [*Kochia scoparia* (L.) Schrad.], and common cocklebur, are at risk for developing glyphosate resistance where glyphosate is applied continually over time and space (Powles 2008a). Despite the prevalence of GT and GR weeds, glyphosate use will likely continue because it effectively controls many other weed species that are present in the soil seedbank. The occurrence of triazine-resistant weeds in corn (*Zea mays* L.) presents growers with a similar problem (Shaner 1995). In many instances, triazine-resistant weed species are managed by adding herbicides with other modes of action to the triazine-based management system.

There is a general assumption that management factors that effectively minimize selection pressure for GR weed species will also be effective in reducing the potential for fields to be dominated by GT weed species. The following discussion of glyphosate stewardship will focus on GR weed species, but will most likely be applicable to GT weeds as well. In an effort to manage GR Palmer amaranth and minimize the selection

pressure and occurrence of additional GT and GR weed species, growers have begun to incorporate other weed control practices into their production systems, including multiple herbicide tank mixtures and cultivation. The application of herbicides with different modes of action in mixtures is likely to have a large impact in delaying the development of herbicide resistance (Jasieniuk et al. 1996). Over a 20-yr corn monoculture, the occurrences of triazine-resistant weeds in systems with mixtures of chloroacetamides with triazines were rare relative to triazine-only systems (Wrubel and Gressel 1994). In entomology, research has demonstrated that the rate of resistance development in insects is slowed when insecticides are applied in mixtures (McGaughey and Johnson 1992; McKenzie and Byford 1993; Prabhaker et al. 1998; Tao et al. 2006).

The reintroduction and maintenance of sufficient diversity of weed management strategies within an agricultural system should slow the rate of (or even prevent) development of herbicide resistance, and will be required to preserve glyphosate as a weed control tool (Powles 2008a). However, not all glyphosate-alternative herbicide mixtures will be equally robust in reducing selection pressure across a multitude of weed species (Beckie 2006; Boerboom 2007). For instance, Palmer amaranth and johnsongrass [*Sorghum halepense* (L.) Pers.] are two species with biotypes that are resistant to glyphosate in the southeastern United States (Heap 2008). An effective glyphosate tank-mixture partner for reducing glyphosate selection pressure on Palmer amaranth (e.g., fomesafen) will likely not be effective in reducing glyphosate selection pressure on johnsongrass. Additionally, herbicide mixtures may actually promote the development of metabolism-based herbicide resistance (Shaner 1999). In Australia, weed biotypes have developed the ability to metabolize herbicides before they reach the herbicide site of action in the plant (Preston et al. 1996). This type of resistance suggests that any type of xenobiotic that is recognized by the plant species can be neutralized before significant plant damage. To date, this mechanism of resistance to glyphosate has not been identified in *Amaranthus* species.

Tragedy of the Commons. The presence of mobile herbicide resistance or herbicide tolerance traits raises questions of how to address management on a grower, county, and regional level (Cardina et al. 1999). The line between individual property rights and collective property rights can become blurred in some instances. Collective property, or a commons, is a resource that is shared by the population. Hardin (1968) and Rankin et al. (2007) described the *tragedy of the commons* as a situation in which the actions, or inactions, of individuals precipitate the collapse of the resource for which they are competing. The tragedy of the commons was initially described by Hardin (1968), who hypothesized that rational individuals would discharge pollutants into a shared water source, instead of using costly measures to purify the waste before release, because of the immediate economic benefit. The tragedy of the commons has been extended to numerous scenarios and disciplines, including evolutionary biology, energy policies, air pollution, management of wildlife and fisheries, ozone depletion, and water usage (Burger and Gochfeld 1998; Lloyd 2007; Rankin et al. 2007).

Gould (1995) suggested that pesticide resistance issues can also be considered a tragedy of the commons, as pesticide

susceptibility is a resource that is openly available to all farmers. Agricultural practices aimed at delaying or preventing the development of herbicide resistance are not viewed as being economical in the short term, and are not readily used by all growers (Beckie 2006; Culpepper 2006; Mueller et al. 2005). Weed-control performance and cost are often of greater importance to growers than site of action when selecting a herbicide (Beckie 2006). Because herbicide resistance can spread quickly, indiscriminate use of glyphosate may result in a loss of weed susceptibility for all growers, a tragedy of the commons (Gould 1995).

Herbicide efficacy is an exhaustible resource for which there has been insufficient stewardship (Beckie 2006; Llewellyn et al. 2007). Stewardship is the sum of the management decisions and practices that are used to preserve the utility of a crop trait (Owen 2007). Stewardship assumes that such practices will be made voluntarily by the grower when it is economically beneficial. Despite increased grower education with respect to glyphosate resistance, the management practices necessary for minimizing the development of herbicide resistance have not been widely implemented (Owen 2007). Awareness of the problem does not always lead to proactive measures. For instance, grower awareness of a herbicide resistance issue in Canada was reported to exceed 90%; however, only 40% of farmers altered their weed control strategy on the basis of this knowledge (Goodwin 1994).

Glyphosate was applied to 12 and 13% of the Georgia and U.S. cotton, respectively, in 1996 (USDA-NASS 1997). The rapid adoption of this technology was apparent by 1999, with 73% of Georgia cotton receiving an application of glyphosate, more than double (36%) that applied to U.S. cotton (USDA-NASS 2000). Glyphosate was applied to 90 and 70% of Georgia and U.S. cotton hectares, respectively, in 2003 and 95 and 91%, respectively, in 2007 (USDA-NASS 2004, 2008). This trend toward indiscriminate use of glyphosate is not restricted to Georgia or cotton production. Of the estimated 100 million ha of transgenic crops grown worldwide, 95% are GR (James 2006; Powles 2008b), including 90 and 60% of U.S. soybean and corn, respectively (Dill et al. 2008). Rapid adoption of GR soybean has also occurred in Argentina and Brazil, accounting for greater than 90% of the crop area (Weersink et al. 2005).

There are at least two factors that may be hindering the adoption of practices that contribute to glyphosate stewardship: (1) the belief that a new technology will be developed to solve the resistance (and tolerance) problems and (2) the belief that resistance management strategies will be futile. Growers who believed that the existing herbicide options would soon be replenished with alternative chemistries were less likely to adopt resistance avoidance strategies compared with those who possessed greater uncertainty about the availability of these alternatives (Llewellyn et al. 2007). This belief is not without precedence. For instance, weeds have developed resistance to several classes of herbicides, including ALS inhibitors, acetyl-CoA carboxylase inhibitors, and triazines. The use of GT cropping systems was an effective means of managing weeds that were resistant to these other classes of herbicides. Although there is a common perception that new herbicides will be developed to address resistance issues, there has not been a new herbicide mode of action introduced commercially since 1998. Many manufacturers abandoned herbicide discovery efforts when GT crops became dominant

and use of other herbicides greatly diminished (J. Gressel, personal communication).

The perception that resistance strategies will be futile is based upon the notion that herbicide resistance traits are mobile. Pollen-mediated transfer of herbicide resistance genes within populations can be a significant factor in allowing for localized spread of resistant weeds. Rates of gene flow are generally thought to be higher than mutation rates, particularly in obligate out-crossing species, such as Palmer amaranth (Jasieniuk et al. 1996). Glyphosate resistance in Palmer amaranth has been shown to spread through pollen movement (Sosnoskie et al. 2007). The message to growers in Georgia has been that failure to manage GR Palmer amaranth not only causes problems on their farms, but on their neighbors' farms as well. A similar scenario has been observed in western Tennessee with movement of seed of GR horseweed from poorly managed farms to neighboring farms (Mueller et al. 2005). In Western Australia, 70% of growers surveyed believed they had gained herbicide-resistant weeds from a neighboring farm because of the movement of seed or pollen (Llewellyn and Allen 2006). A survey of farmer perceptions in Ohio indicated that they attributed weed introductions to their fields from natural elements (e.g., wind, wildlife, water), with 23% of respondents specifically mentioning movement of weeds from their neighbors' poorly managed fields (Wilson et al. 2008). The assumption that growers who invest in resistance management programs will enjoy the benefits (i.e., delayed occurrence of herbicide resistance) on their farm may be inaccurate in many instances (Llewellyn and Allen 2006). Spoiling of the common resource of pesticide susceptibility can make growers reluctant to spend their resources (i.e., time and money) to implement management programs that deter the development of pesticide resistance (Gould 1995).

Hardin (1968) suggested that there were two means of addressing the tragedy of the commons: incentives or actions originating from either (1) the private sector or (2) the public sector. Along these lines, Boerboom (2007) proposed three potential courses of action for fostering glyphosate stewardship: (1) status quo where the use of the technology is dictated by market forces, accepting the development of GR and GT weeds, (2) industry-led initiatives to promote good glyphosate stewardship (e.g., rebates to growers that do not use glyphosate), and (3) incentives from voluntary government farm programs. Manufacturers of glyphosate have developed economic incentives to encourage growers to utilize specific glyphosate tank mixtures as a means of promoting glyphosate stewardship. Herbicides that were strategically premixed to leverage stewardship were effectively implemented by Canadian growers with other types of herbicide resistance (Beckie 2006). The agricultural industry has voiced opposition to mandatory government regulation as a means to promote glyphosate stewardship (Boerboom and Owen 2007; Owen and Boerboom 2004), but the role of government in monitoring and regulating herbicide-resistant weeds has not been clearly defined (Hall et al. 2000). Additional incentives in the form of various social factors, including reputation among the community, have also been proposed as a potential means to affect changes in behavior that encourage stewardship (Milinski et al. 2002; Semmann et al. 2005; Uphoff and Langholz 1998). However, this research topic has not been explored with regard to herbicide resistance.

Glyphosate stewardship should also involve various cultural crop production practices as a means of managing weeds (Cardina et al. 1999). Cultural practices that minimize additions of weeds to the soil seedbank and maximize seed or seedling mortality are the focus of ecological weed management (Bastiaans et al. 2008). Ultimately, weed population densities within the soil seedbank must be reduced. There are three critical stages within the life cycle of a weed: (1) seedling establishment, (2) seed production, and (3) persistence of the soil seedbank (Anderson 2005). Weed management strategies, whether herbicide intensive or ecologically based, should target one of the transitions between these stages. Principles of ecological weed management used in conjunction with herbicide-based weed control systems will likely be an important component of future weed management systems.

Conclusion. Glyphosate susceptibility in the most frequently occurring and troublesome weed species is a common resource that is rapidly being lost in Georgia because of an overall lack of stewardship. There are genera that possess a natural tolerance to glyphosate, including *Commelina* spp., *Polygonum* spp., and *Ipomoea* spp. As a group, pigweeds are naturally sensitive to glyphosate. However, pigweeds have demonstrated the ability to develop resistance to numerous herbicide classes, including ALS inhibitors, protoporphyrinogen oxidase inhibitors, dinitroanilines, glyphosate, and triazines (Heap 2008; Vencill et al. 2008). Once developed, pesticide resistance is usually a persistent trait in the population that does not diminish once the pesticide use is halted (Jasieniuk et al. 1996; Owen 2007). With the occurrence of GR Palmer amaranth in Arkansas, Mississippi, North Carolina, South Carolina, and Tennessee (Culpepper et al. 2008b; Norsworthy et al. 2008; Steckel et al. 2008), it is likely that these states will follow the same path as Georgia and similarly endanger glyphosate susceptibility in Palmer amaranth. Greater understanding of the means by which heritable traits provide an advantage for survival of weeds in agroecosystems, including, but not limited to, herbicide resistance, will allow us to provide more complete information to growers on improved stewardship and weed management systems. As development of new technologies continues for crop production (e.g., dicamba- or 2,4-D-resistant cotton cultivars, or other new technologies), it will be more important to wisely use these advances and be better stewards over these traits, instead of compromising them as we have done with glyphosate.

There are a multitude of questions that can be addressed through research to improve our understanding of herbicide resistance and weedy traits. Although not an exhaustive list, answers to the following questions would assist us in providing improved stewardship of future technologies: (1) what is the most effective means of mitigating the risk of the development of herbicide-resistant and herbicide-tolerant weeds? (2) Will herbicide mixtures that include glyphosate (or other herbicide of interest) minimize the risk of resistant and tolerant weeds, or will glyphosate use need to be limited to once a season (or less)? (3) Are there factors (e.g., cultural practices, physical weed control, or biological control) that can improve control and stewardship of current herbicide options? (4) How do herbicide resistance traits move and how mobile are they across the landscape? (5) Are there basic factors that can be used to access the risk of a species to develop resistance so that we can target our programs to

reduce the risk of selecting for resistance? (6) What types of incentives could be implemented to improve herbicide stewardship and promote herbicide susceptibility in weed populations? Answers to the complex question of how to avoid repeating these mistakes will likely require the entire agricultural community (i.e., growers, consultants, county agents, public scientists, and the agricultural industry) to generate and apply knowledge of weed science (both basic and applied), evolutionary biology, economics, and sociology.

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